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REVERSIONARY CHARACTERS OF TRAUMATIC OAK WOODS¹

IRVING W. BAILEY

(WITH PLATES XI AND XII)

In studying the phylogeny of plants there are certain principles or canons of comparative anatomy which have been formulated within recent years by morphologists and anatomists. Thus the application, to seedling plants, of HAECKEL'S law of recapitulation for stages in ontogenesis has been strikingly illustrated by STRASBURGER, GOEBEL, JEFFREY, EAMES, and others. Furthermore, the persistency of ancestral characters in certain regions of plants has been well established. In this connection the researches of SOLMS-LAUBACH, SCOTT, and JEFFREY have shown conclusively that the cone axis is often the seat of primitive characters. The importance of foliar organs in connection with ancestral characters has been shown by SCOTT, JEFFREY, and FAULL. JEFFREY has further pointed out in his memoir on *Sequoia*² the importance of vigorous cone-bearing branches of *Sequoia gigantea* as the seat of recapitulation of ancestral conditions. The importance of hypertrophied or wounded areas as the seat of reversion to primitive characters is strongly appreciated by zoologists. This principle has also been applied to the traumatic areas of plants by JEFFREY, who has pointed out the traumatic reversionary origin of resin canals in the wood of the higher Abietineae,³ certain Sequoiineae,⁴ and the older Araucarineae,⁵ which normally possess none of these

¹ Contributions from the Phanerogamic Laboratories of Harvard University, no. 24.

² The comparative anatomy and phylogeny of the Coniferales. I. The genus *Sequoia*. Mem. Boston Soc. Nat. Hist. 5:441-459. pls. 68-71. 1903.

³ The comparative anatomy and phylogeny of the Coniferales. II. The Abietineae. Mem. Boston Soc. Nat. Hist. 6:1-37. pls. 1-7. 1904.

⁴ The comparative anatomy and phylogeny of the Coniferales. I. The genus *Sequoia*. Mem. Boston Soc. Nat. Hist. 5:441-459. pls. 68-71. 1903.

⁵ The wound reactions of *Brachyphyllum*. Annals of Botany 20:383-394. pls. 27, 28. 1906.

Araucariopitys, a new genus of araucarians. BOT. GAZETTE 44:435-444. pls. 28-30. 1907.

structures; and has demonstrated the presence of traumatic marginal tracheids in the wounded wood of *Cunninghamia sinensis*.⁶

An interesting parallel to the work of JEFFREY upon traumatic reversions in the Coniferales has been noted by the writer in the traumatic reversions of wounded oak wood. Owing to the controversy which exists as to the relative primitiveness of the Abietineae and Cupressineae this occurrence of traumatic reversions in a dicotyledonous genus is of particular interest in demonstrating the application of the principles of experimental morphology to plants.

Before describing the reversionary characters of oaks, it will be well to have clearly in mind the normal structure of the wood of existing oaks, and also that of ancestral types. As is well known, the secondary xylem of living oaks consists of vessels, fibers, tracheids, and parenchyma. The last occurs vertically as wood parenchyma, and horizontally disposed in plates of tissue extending radially, the so-called primary and secondary medullary rays. The "primary rays" (fig. 1) are the distinctive feature of oak wood, the "silver grain," and are broad, fusiform masses, many cells in width, which are supposed to originate as inclusions of fundamental tissue between the primary fibrovascular bundles. The "secondary rays" are thin sheets of tissue, and consist of a single row of cells when seen in tangential or transverse section (fig. 1). These rays, unlike the primary rays, are supposed to originate only with secondary growth.

In contrast to this type of structure occurring in the mature wood of extant oaks, EAMES has shown⁷ that certain miocene oaks do not possess large rays composed of homogeneous masses of ray parenchyma, but have in their place bands of aggregated smaller rays which are separated by fibers and wood parenchyma. These rays are homologous with the "false rays" of the Betulaceae, and lead to the conclusion that the so-called primary rays of extant oaks have been built up by an aggregation and fusion of numerous originally uniseriate rays.

⁶ Traumatic ray tracheids in *Cunninghamia sinensis*. *Annals of Botany* 22:593-602. *pl.* 31. 1908.

⁷ On the origin of the broad ray in *Quercus*. *BOT. GAZETTE* 49:161-166. *pls.* 8, 9. 1910.

The writer has shown,⁸ by a study of numerous species of Betulaceae and Fagaceae, that ample evidence of a compounding process exists in the rays of many living oaks, alders, birches, and hornbeams. Thus many American live oaks (fig. 5) possess bands of aggregated rays which are similar to the false rays of the Betulaceae. Among alders and birches species may be found with non-aggregated uniseriate rays, aggregated small rays, and large homogeneous rays like the so-called primary rays of oak. In fact, in the genus *Alnus* species may be found which form a perfect series of transitional steps between alders with non-aggregated uniseriate rays and *Alnus rhombifolia* Nutt., which often possesses large compound rays such as are found in the higher oaks.

Further, EAMES has shown that in the development of seedling oaks a similar series of stages occur. Thus in seedlings of *Quercus alba* L. and *Q. rubra* L., which in the adult possess broad homogeneous rays, the first-formed wood resembles the adult wood of chestnut in possessing non-aggregated uniseriate rays. In the further growth of the young plant, aggregations of rays develop, which by subsequent fusion constitute the large rays of the mature wood.

Thus three lines of evidence, afforded by the study of seedling stages, fossil ancestral forms, and the development of ray structures in living forms, show conclusively that the wood of primitive Fagaceae and Betulaceae was characterized by the entire absence of large medullary rays. With the development of unequal seasonal temperatures, a highly organized storage system for foods became advantageous to plants, and the large rays of modern oaks have been evolved by an aggregation and fusion of numerous uniseriate rays to meet this demand.

With these preliminary statements on the normal and ancestral features of oak wood, we may now turn to a more detailed consideration of the abnormal structures which exist in traumatic oaks. It has been pointed out above that traumatic regions are often the seat of ancestral characters and show a series of stages similar

⁸ Relation of the leaf trace to the origin and development of compound rays in the dicotyledons. *Annals of Botany*. *Ined.*

to embryonic or seedling stages. We should accordingly expect to find in wounded oak wood a reversion to primitive ray structure. That this reversion does occur has been shown conclusively by the examination of numerous areas of wounded oak wood. In fact, in all cases a complete series of transitional stages in the development of compound rays occurred, resembling the series of steps found by EAMES in the development of seedling plants. The wood formed immediately after wounding possesses characteristically only uniseriate rays. In following layers aggregations of the rays develop, with subsequent enlargement of the uniseriate rays, and their subsequent fusion into homogeneous masses or compound rays. During this compounding process, fibers and wood parenchyma included in the fusing mass are transformed into ray parenchyma.

In all cases, in securing material, burls and distorted tissues were carefully avoided and straight-grained traumatic tissue selected.

In fig. 1 may be seen a tangential section of the normal adult wood of *Quercus nigra* L. The so-called primary and secondary rays are characteristically developed; the former consists of a homogeneous mass of ray parenchyma. In contrast to this the traumatic wood of the same species may be seen in fig. 2. The large ray is seen to consist of a compounding mass of smaller rays.

Figs. 3 and 4 illustrate the normal and traumatic condition in *Quercus virginiana* Mill., the important live oak of the southern United States. As may be seen, in this species the normal adult wood is characterized by an imperfectly compounded ray. Numerous included fibers and wood parenchyma cells, evidences of fusion, are usually present. Fig. 4 illustrates the reversion of the wood in the vicinity of the wound to the non-aggregated uniseriate condition.

In figs. 5 and 6 are shown sections of the normal and the traumatic wood of *Quercus densiflora* Hook. and Arn., a live oak whose normal adult wood is characterized by large rays in which the process of compounding is clearly shown. The wounded wood of the species reverts to a more primitive type of compounding, as may be seen in fig. 6.

Figs. 7-10 illustrate the normal and traumatic wood of the well known *Quercus alba*, a deciduous oak with highly specialized ray structure. Figs. 8 and 10, tangential and transverse sections respectively of the traumatic wood, show that this species also reverts to ancestral type of ray structures.

This reversion to ancestral conditions has been found by the writer in woody tissues subsequent to severe injury. Slight injuries, on the other hand, particularly in oaks with highly specialized ray structure, often produce no morphological effect upon the wood. In a limited number of cases very slight wounds have produced a stimulation of the compounding tendency or acceleration of development rather than a reversion to ancestral structures. In fig. 11 may be seen a cross-section of *Alnus* sp. The lower portion of the figure shows none of the so-called false rays, but in the upper half numerous rays have developed abruptly outside a zone indicating slight injury. Fig. 12 shows a similar phenomenon in the young stem of *Quercus densiflora*. In the lower half may be seen normal seedling wood in which only uniseriate rays occur. Starting from a zone of slight injury in the middle of the section, a compound ray has suddenly appeared in the upper portion of the figure. From this we see that very slight injuries produce an acceleration in the formation of compound rays.

SUMMARY AND CONCLUSIONS

1. The phylogenetic importance of traumatic areas as the seat of reversion to primitive structures is well illustrated by the specimens of wounded oak wood which have been examined by the writer.
2. In traumatic wood progressive stages are found which are similar to the stages of recapitulation found in the seedling, and equivalents to the condition found in adult miocene oaks.
3. Woody tissues in the immediate vicinity of a severe wound show only non-aggregated uniseriate or small rays. In subsequently formed tissues the gradual building up of the compound ray may be traced in a consecutive series of steps to the normal homogeneous large ray of the adult wood.
4. On the basis of traumatic and developmental as well as paleo-

botanical evidence, the large homogeneous masses of ray parenchyma, or the so-called primary rays of oaks with deciduous foliage, appear to have been built up by an aggregation and fusion of numerous uniseriate rays.

5. Traumatic reversions are confined to regions which have been severely injured. Occasionally areas where the traumatic effect has been slight show an acceleration of the compounding process instead of a reversion to ancestral stages.

6. The so-called primary ray is seen to have originated from an aggregation and fusion of secondary rays, and to be in no way related to inclusions of fundamental tissue between the primary fibrovascular bundles. From this phylogenetic relation of the two sorts of medullary rays it seems that the term primary is inadmissible entirely for the large rays of oak, and that the term *compound* might be advantageously substituted.

In conclusion I wish to express my sincere thanks to Mr. G. B. SUDWORTH, dendrologist of the U.S. Forest Service, for material of *Alnus rhombifolia*. I am also much indebted to Professor E. C. JEFFREY for suggestions and advice, and to Mr. A. J. EAMES for material of several wounded oaks.

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EXPLANATION OF PLATES XI AND XII

PLATE XI

FIG. 1.—*Quercus nigra*: tangential section of the normal adult wood, showing the so-called primary and secondary rays; the former are seen to consist of large masses of homogeneous ray parenchyma; $\times 120$.

FIG. 2.—*Quercus nigra*: tangential section of the traumatic wood, showing compounding mass of small rays; $\times 120$.

FIG. 3.—*Quercus virginiana*: tangential section of the normal adult wood, showing strong evidences of a compounding process; inclusions of fibers and wood parenchyma cells occur conspicuously; $\times 120$.

FIG. 4.—*Quercus virginiana*: tangential section of the traumatic wood, showing uniseriate non-aggregated rays in the immediate vicinity of a severe wound; $\times 120$.

FIG. 5.—*Quercus densiflora*: tangential section of the normal adult wood, showing aggregating and fusing mass of small rays; $\times 60$.

FIG. 6.—*Quercus densiflora*: tangential section of the traumatic wood, showing aggregation of uniseriate and biseriate rays; $\times 120$.

PLATE XII

FIG. 7.—*Quercus alba*: tangential section of the normal adult wood, showing highly organized broad homogeneous ray; $\times 120$.

FIG. 8.—*Quercus alba*: tangential section of the traumatic wood, showing the aggregation and fusion of triseriate and biseriate rays; these rays have been produced by the enlargement or growth in diameter of uniseriate rays; $\times 120$.

FIG. 9.—*Quercus alba*: transverse section of the normal adult wood, showing the highly organized type of ray; $\times 120$.

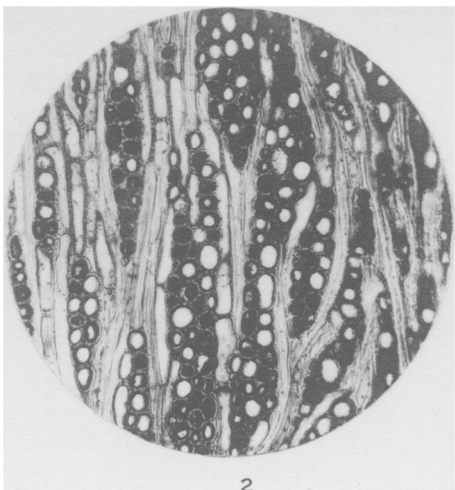
FIG. 10.—*Quercus alba*: transverse section of the traumatic wood, showing aggregation of uniseriate, biseriate, and triseriate rays; $\times 120$.

FIG. 11.—*Alnus* sp.: transverse section of very slightly injured wood; compounding rays are absent from the lower half of the section; starting abruptly from a line of slightly injured tissue which crosses the middle of the section, numerous rays extend outward to the exterior of the stem; $\times 40$.

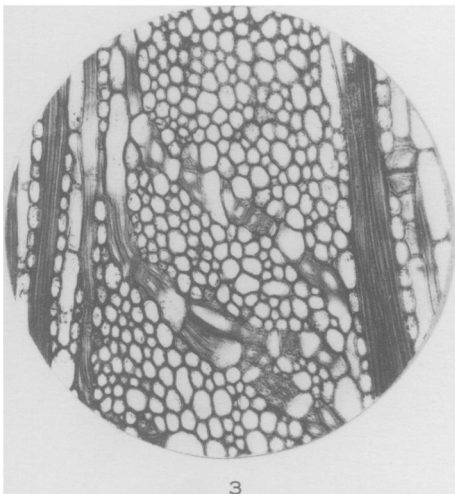
FIG. 12.—*Quercus densiflora*: transverse section of very slightly injured wood; the lower half of the section possesses only uniseriate rays, but starting from the middle of the section a compounding ray has originated from a slight injury to the wood; $\times 60$.



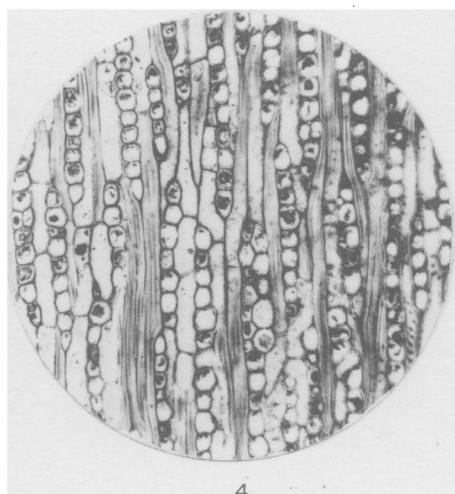
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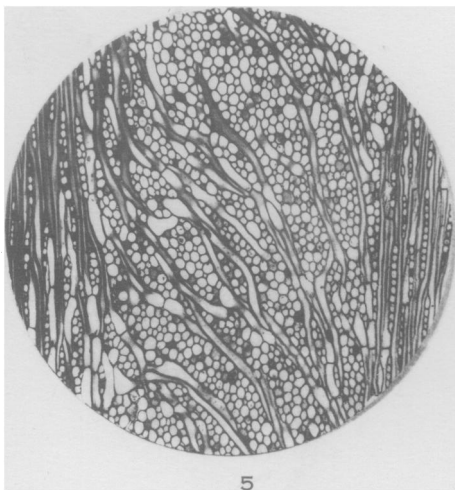
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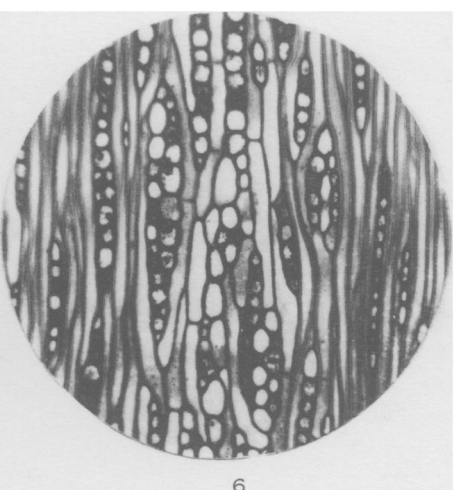
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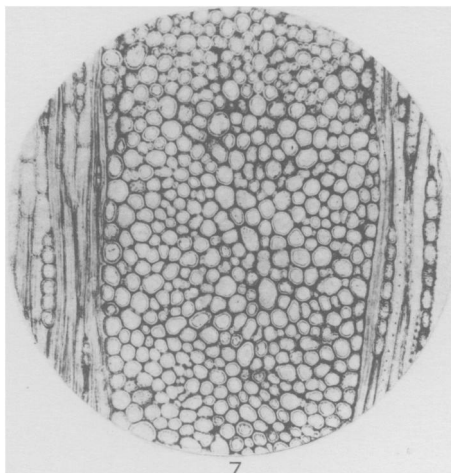
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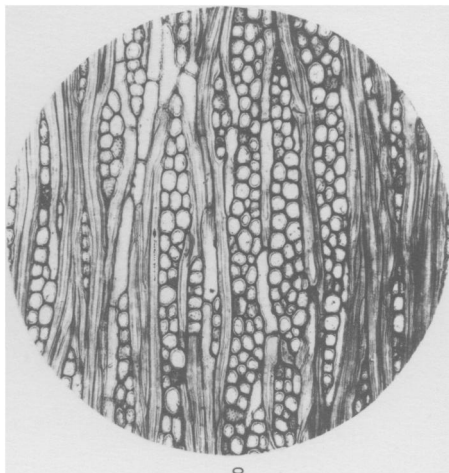
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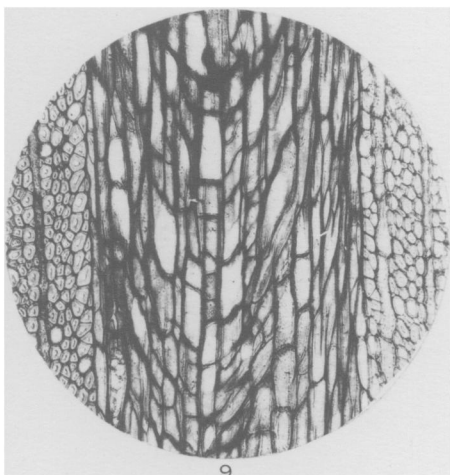
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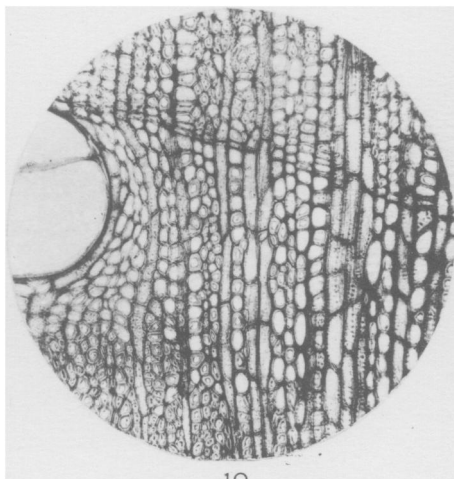
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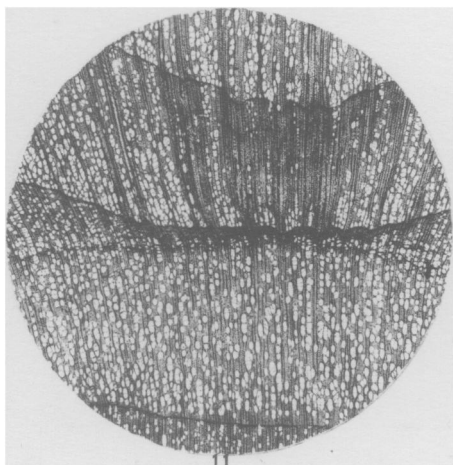
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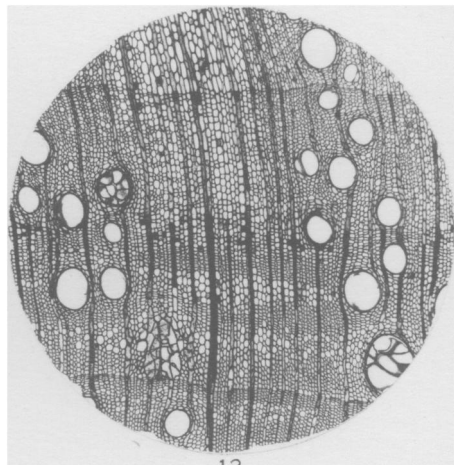
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